AMERICAN MUSEUM
Novitates

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, N.Y. 10024
Number 2988, 21 pp., 12 illustrations, 3 tables October 25, 1990

A New Poison Frog from Amazonian Brazil, with Further Revision of the *quinquevittatus* Group of *Dendrobates*

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ABSTRACT

Dendrobates castaneoticus, new species, is a brilliantly colored small (18–23 mm SVL) poison frog from lowland rain forest in Pará, Brazil. It is black, with vivid white spots or short lines on the body and bright orange markings on the limbs. Its sister species seems to be *Dendrobates quinquevittatus* sensu stricto, a smaller and differently patterned frog.

Dendrobates castaneoticus and *D. quinquevittatus* share a possibly novel synapomorphy within the Dendrobatidae (inner metacarpal tubercle absent or vestigial) and have virtually identical tadpoles. Both species use adventitious phytotelmata on and near the forest floor for deposition of tadpoles, but fallen rain-filled fruit capsules of the Brazil nut tree (*Bertholletia excelsa*, Lecythidaceae) seem to provide an especially important larval habitat. The calls and courtship behavior are unknown. *Dendrobates quinquevittatus* produces toxic alkaloids mainly of the histrionicotoxin and pumiliotoxin-A classes; no data are available for *D. castaneoticus*.

The name *Dendrobates quinquevittatus* Steindachner, 1864, misapplied in recent literature, is severely restricted to a species that is neither as variable nor as widespread as previously thought; it is known only from the upper Rio Madeira drainage of Rondônia and adjacent (southern) Amazonas, Brazil. The name *Dendrobates ventrimaculatus* Shreve, 1935, is to be used for the diverse populations recently assigned to *quinquevittatus*, but it is a composite species whose successful taxonomic treatment will depend on thorough studies of intrapopulational and geographic variation in all accessible characters. *Dendrobates variabilis* Zimmermann and Zimmermann, 1988—from somewhere (no explicit type locality) in Depto. San Martín, Peru—probably is applicable to a distinct species in this complex, but the name is referred to synonymy until sufficient evidence is available to differentiate it from other populations of *D. ventrimaculatus* sensu lato.

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ISSN 0003-0082 / Price $3.55

RESUMEN

Dendrobates castaneoticus, especie nueva, es una pequeña y espectacular rana venenosa de la selva pluvial baja del Pará, Brasil. Es negra con manchas o líneas cortas blancas sobre el cuerpo y manchas grandes anaranjado brillantes sobre los miembros. Su especie hermana parece ser *Dendrobates quinquevittatus* sensu stricto, una rana más pequeña y con un patrón de coloración diferente.

Dendrobates castaneoticus y *D. quinquevittatus* comparten una sinapomorfía posiblemente singular entre los Dendrobatidae (tubérculo metacarpal interno ausente o rudimentario) y tienen larvas muy similares. Ambas especies usan agua de lluvia en fitotelmata adventicios sobre y cerca de la tierra para el depósito de las larvas, pero también las cápsulas caídas de las frutas del castaño del Brasil (*Bertholletia excelsa*, Lecythidaceae) parecen proveer un ambiente larval especialmente importante. El canto y el cortejo se desconocen. *D. quinquevittatus* produce alcaloides tóxicos, principalmente de las clases histrionicotoxina y pumiliotoxina-A; no existen datos disponibles para *D. castaneoticus*. El nombre *Dendrobates quinquevittatus* Steindachner, 1864, incorrectamente aplicado en la literatura reciente, está restringido severamente a una especie que ni es tan variable ni tan ampliamente distribuida como previamente se pensaba; se conoce solamente del drenaje alto del Río Madeira en estado Rondônia y del adyacente (meridional) estado Amazonas, Brasil. El nombre *Dendrobates ventrimaculatus* Shreve, 1935, se debe usar para los poblaciones diversas que recientemente se han asignado a *quinquevittatus*, pero ésta es una especie compuesta cuyo próspero trato taxonómico dependerá en estudios completos de variación dentro de poblaciones y de variación geográfica en todos los caracteres accesibles. *Dendrobates variabilis* Zimmermann y Zimmermann, 1988—de alguna parte del Depto. San Martín, Perú (ninguna localidad tipo explícita)—probablemente es aplicable a una especie distinta de este complejo, pero el nombre se refiere a sinonimia hasta que haya evidencia suficiente para diferenciar ésta de las otras poblaciones de *D. ventrimaculatus* sensu lato.

INTRODUCTION

In 1987, the first author and her field associates obtained specimens and information on a strikingly colored small poison frog in Pará, Brazil, in undisturbed primary rain forest. The breeding biology of this species is noteworthy in that rain-filled fruit capsules of the Brazil nut tree (*Bertholletia excelsa*) are frequently used as deposition sites for its tadpoles.

Specimens and preliminary data obtained by the authors and R. I. Crombie a few years earlier, in Rondônia, Brazil, had revealed a similar use of Brazil nut fruit capsules by *Dendrobates quinquevittatus*. Subsequent study revealed that, despite strikingly different color patterns, the new species and *quinquevittatus* are united through shared presence of an iridescent orange or golden spot at the limb insertions and shared absence of the inner metacarpal tubercle—the latter a novel synapomorphy in the Dendrobatidae.

Our work in Rondônia also led to a realization that the name *Dendrobates quinquevittatus* Steindachner (1864) has been misapplied in recent literature. Myers (1982) had partially revised *D. quinquevittatus* sensu lato by showing that it represented a complex of distinct species, some of which were described or removed from synonymy. We continue that revision by severely restricting the name *quinquevittatus* to a species that is neither as variable nor as widely distributed as previously thought, and by applying the next oldest name to the residual populations.

ACKNOWLEDGMENTS

Our work in Brazil was done on faunal survey programs in collaboration with the Museu de Zoologia, Universidade de São Paulo, on behalf of Eletronorte, the federal agency in charge of energy generation in Amazonia. We thank Dr. Paulo Emilio Vanzolini for making this possible.

For assistance in collecting specimens of the new frog from Pará, the first author thanks Laurie J. Vitt, Jeffrey M. Howland, Pamela T. Lopez, Guarino Rinaldi Colli, and João Silva de Oliveira. Their fieldwork was greatly facilitated by the staff of Acampamento Ju-

ruá, established by the Consorcio Nacional de Engenheiros Consultores S.A., and used as home base, with special thanks to Pedro Ianibelli, Vilmar José de Queiroz, João Baptisto Filho, and José Antonio Cunha. Maria Beatriz Ribeiro do Valle provided indispensable logistical help.

Ronald I. Crombie collaborated on fieldwork in Rondônia and kindly made his notes available on *Dendrobates quinquevittatus*. Martin Henzl provided information on the holotype of *D. quinquevittatus*. Roy W. McDiarmid and Rex B. Cocroft called our attention to an interesting sample of frogs from Tampopata, Peru. For reading the manuscript, we thank Ronald I. Crombie, P. E. Vanzolini, and Laurie J. Vitt. Dr. Vitt also deserves special acknowledgment for suffering the painful sting of a large scorpion (*Centruroides*) while catching the holotype of the new frog—expected behavior in a field biologist but appreciated nonetheless.

Abbreviations

Collection abbreviations used in this paper are:

AMNH	American Museum of Natural History, New York
MCZ	Museum of Comparative Zoology, Harvard University
MZUSP	Museu de Zoologia, Universidade da São Paulo
NMW	Naturhistorisches Museum, Vienna
SMNS	Staatlichen Museum für Naturkunde in Stuttgart
USNM	National Museum of Natural History, Smithsonian Institution, Washington, D.C.

Dendrobates castaneoticus, new species

Figures 1–4, 5A, 6A, 8A

HOLOTYPE: MZUSP 64775 (field no. JPC 7115), an adult female caught by Laurie J. Vitt on February 24, 1987, in primary lowland rain forest near Cachoeira Juruá, Rio Xingu, State of Pará, Brazil. The type locality is approximately 03°22′S, 51°51′W on the international millionth map (sheet SA-22[3]); the site is situated within a loop of the Rio Xingu, about 220 km S of its junction with the Rio Amazonas.

PARATYPES: A total of 18 specimens, all from northern Pará, as follows: MZUSP 30767, 35681, from Taperinha (02°32′S, 54°17′W), about 48 km ESE Santarém, collected by H. Reichardt, February 1–11, 1968, and by P. E. Vanzolini, October 22, 1970, respectively. MZUSP 64763–64771, 64777, AMNH 133451–133455, from the type locality, and MZUSP 64776 from 13 km NW of the type locality; preceding specimens collected January 18–March 5, 1987, by Janalee P. Caldwell, Guarino Rinaldi Colli, Jeffrey M. Howland, Pamela T. Lopez, João Silva de Oliveira, and Laurie J. Vitt.

ETYMOLOGY: The species name is derived from the Latin/Portuguese *castanea/castanha* (chestnut) + the Latin adjectival suffix *-(t)icus* (belonging to); the connective *o* (rather than the usual Latin *i*) is inserted for euphony.

The allusion is not to the European chestnut tree (*Castanea*) but rather to the tropical South American Brazil nut tree (*Bertholletia excelsa*, Lecythidaceae), whose Brazilian common name is "Castanha do Pará." Although this tree is widely distributed outside of Pará, its frog namesake is not. Fallen water-filled fruit capsules of the Castanha do Pará appear to be an important habitat for the larvae of *Dendrobates castaneoticus* of Pará.[4]

DIAGNOSIS: *Dendrobates castaneoticus* is a small to medium-size toothless dendrobatid (about 18–23 mm SVL) with appressed first finger shorter than second and lacking an inner metacarpal tubercle. The new species differs from all other dendrobatids in its distinctive, albeit variable, color pattern of vivid

[3] *Carta do Brasil (1:1,000,000)*. Instituto Brasileiro de Geografia, 1972 (2nd ed.).

[4] In Brazil, the word *castanha* by itself refers to one of the edible seeds, whereas the smooth woody fruit capsule or pyxidium is inappropriately called *ouriço* (meaning hedgehog, after the prickly covering of the European chestnut, fide P. E. Vanzolini, personal commun.).

The seeds are larger in diameter than the fruit opening and therefore remain in the fallen fruit, which typically is gnawed open by an agouti (*Dasyprocta*) that eats some seeds and buries others (Mori and Prance, 1987). The empty woody capsule may then fill with rainwater and provide a transient microhabitat for tadpoles, mosquito larvae, and other small organisms.

Fig. 1. *Dendrobates castaneoticus*, new species. One of the paratopotypes (MZUSP 64764) shown in life, approximately ×3; from a color transparency by J. P. Caldwell.

white and brilliant orange markings on a black field (figs. 1, 3): the pale markings on the body are white, those on the limbs are orange.

The somewhat similar *D. vanzolinii* differs in having yellow body spots, pale reticulated limbs, and a distinct inner metacarpal tubercle (cf. Myers, 1982, figs. 4B, 6–7). The derived absence of a metacarpal tubercle is shared by *D. castaneoticus* and *D. quinquevittatus* sensu stricto, but the latter has a very different dorsal color pattern except for the shared presence of an iridescent orange or golden spot at the dorsal limb insertions (cf. figs. 1, 7).

MEASUREMENTS (in mm) OF HOLOTYPE: The holotype (fig. 3B) is an adult female with mature ovaries and enlarged oviducts; it has a supernumerary digit on the underside of toe 3 of the right foot but appears normal in all other respects. Length from snout to vent 21.5; tibia length between heel and outer surface of flexed knee 8.6; greatest width of body 8.5; head width between angles of jaws, and between outer edges upper eyelids, 6.8, 6.3 respectively; approximate width of interorbital area 2.7; head length (sagittal) from tip of snout to angle of jaw 5.2; tip of snout to center of naris (sagittal) 0.8; center of naris to anterior edge of eye 2.0; distance between centers of nares 3.0; eye length from anterior to posterior edge 2.6; horizontal diameter of tympanum roughly 1.2; corner of mouth to lower edge of tympanic ring 0.8; hand length from proximal edge of large medial palmar tubercle to tip of longest (third) finger 5.1; width of disc of third finger (and width of penultimate phalanx below disc) 0.9 (0.5); width of discs (and penultimate phalanges below discs) of third and fourth toes 0.7 (0.5) and 0.8 (0.5), respectively.

DESCRIPTION OF TYPE SERIES

The following description is based on 17 adult paratypes and two juvenile paratopotypes. Data on size and proportions of 15 adult frogs from the type locality and vicinity are summarized in table 1. One adult male and one adult female from a more distant locality (Taperinha) agree well with table 1 and are separately discussed only under Color Pattern.

A small to medium-size *Dendrobates*, about 18–23 mm SVL, with females averaging about 2.5 mm larger than males (table 1). Males with shallow, subgular vocal sac; one or two males with vocal slits fully open, but usually one vocal slit (either left or right) is undeveloped or but partially open.[5] Teeth absent.

[5] A not uncommon condition in dendrobatids. Although vocal slits define the presence of a vocal pouch, they are not essential for sound production and have

TABLE 1
Size and Proportions of Adult *Dendrobates castaneoticus*, New Species, from the Type Locality[a]

Character	N	Mean ± 1 SE	SD	CV (%)	Range
Snout–vent length (SVL) in mm	9 ♂	19.32 ± 0.26	0.77	4.00	17.9–20.3
	6 ♀	21.90 ± 0.19	0.46	2.08	21.5–22.7
Tibia length[b]/SVL	9 ♂	0.419 ± 0.003	0.008	1.97	0.40–0.43
	6 ♀	0.401 ± 0.004	0.010	2.51	0.39–0.41
Head width[c]/SVL	9 ♂	0.321 ± 0.002	0.006	1.77	0.31–0.33
	6 ♀	0.319 ± 0.002	0.005	1.56	0.31–0.33
Center naris-edge eye/eye length	9 ♂	0.746 ± 0.025	0.074	9.87	0.65–0.86
	6 ♀	0.747 ± 0.023	0.056	7.45	0.69–0.85
Hand length[d]/SVL	9 ♂	0.258 ± 0.002	0.005	2.09	0.25–0.27
	6 ♀	0.244 ± 0.002	0.005	2.25	0.24–0.25
Hand length/head width	9 ♂	0.803 ± 0.005	0.016	1.96	0.78–0.83
	6 ♀	0.766 ± 0.007	0.018	2.33	0.74–0.79
Width 3rd-finger disc/finger width below disc[e]	8 ♂	2.225 ± 0.045	0.128	5.76	2.00–2.40
	6 ♀	1.939 ± 0.039	0.095	4.91	1.80–2.00

[a] Sample for this table includes a male paratype from 13 km NW of type locality plus 14 adult paratopotypes.
[b] Tibia length in this paper is the shank measured from the heel to the convex surface of the knee (with limb segments flexed at right angles), roughly approximating the length of the tibiofibula.
[c] Greatest head width as measured between jaw articulations.
[d] Hand length measured from proximal edge of large medial palmar tubercle to tip of longest (3rd) finger.
[e] Digit width measured near distal end of penultimate phalanx.

EXTERNAL MORPHOLOGY: Dorsal skin finely granular or smooth in preservative, ventral skin smooth or moderately granular on belly. Head narrower than body; width between angles of jaws 56–95 percent of greatest body width, without clear sexual dimorphism ($\bar{x}$ = 78%, range 56–95% in 9♂; $\bar{x}$ = 73%, range 64–80% in 6♀). Head width 31–33 percent of SVL in adults (table 1), 35–39 percent in two juveniles (12.7 mm and 12.3 mm SVL, respectively). Width between outer edges of upper eyelids only slightly smaller than (< 0.5 mm) or occasionally equal to head width between jaw articulations. Snout sloping, rounded in profile, broadly rounded to nearly truncate in dorsal or ventral view. Nares situated near tip of snout and directed posterolaterally; both nares visible from front and from below, not visible from above. Canthus rostralis rounded; loreal region vertical and slightly concave. Interorbital area wider than upper eyelid. Eye nearly equal to snout length in lateral view; distance from naris to eye 65–86 percent of eye length in adults (table 1), 60–68 percent in two juveniles. Tympanum variably concealed dorsally and posterodorsally, much smaller than eye.

Hand (fig. 2) of moderate size, 24–27 percent of SVL, 74–83 percent of greatest head width in adults (table 1); hand smaller relative to head width in two juveniles (hand/head = 0.69 in each) but similar relative to body size (hand/SVL = 0.25–0.27). Relative length of *appressed* fingers 3 > 4 > 2 > 1; appressed first finger relatively long, its tip usually reaching or slightly overlapping disc of second finger although falling well short of second-finger disc in a few individuals. Discs markedly expanded on all except first finger. Third finger disc 1.8–2.4 times wider than distal end of adjacent phalanx, averaging wider in males than in females (table 1); third finger disc only 1.5 times finger width in two juveniles. All specimens with a single metacarpal tubercle—i.e., a circular to elliptical outer metacarpal tubercle present on base of palm, but inner metacarpal tubercle absent (figs. 2, 8A). One or two rounded subarticular tubercles (two on finger 3, one each on fingers 1, 2, and 4, sometimes with weak indication of a distal second tubercle on finger 4). Ventrolateral edges of digits slightly keeled, with keel from outer edge of finger 4 sometimes extending weakly onto hand nearly to metacarpal tubercle.

been noted as completely absent in one population and in some individuals of two other species in the *Dendrobates quinquevittatus* complex (Myers, 1982: 5).

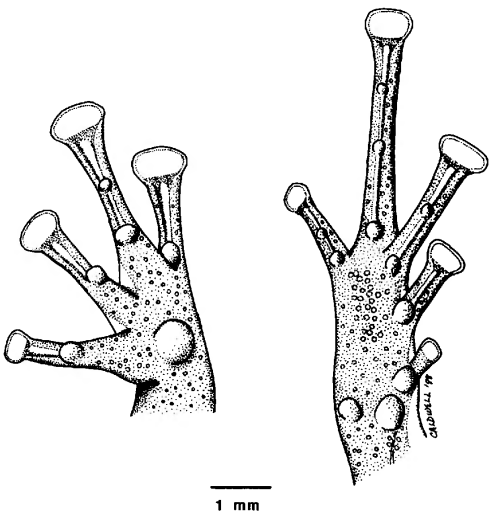

Fig. 2. Left hand and right foot of *Dendrobates castaneoticus*, new species. MZUSP 64763, an adult male paratopotype, ×7.5.

Hind limbs relatively short, with heel of appressed limb usually reaching or almost reaching tympanum, occasionally reaching rear of eye. Tibia length 39–43 percent of SVL in adults (table 1), 43–44 percent in two juveniles. Toes not webbed (fig. 2). Relative lengths of appressed digits 4 > 3 > 5 > 2 > 1; first toe short, barely reaching proximal edge of subarticular tubercle of second toe. First toe with nonexpanded disc, other toes with discs expanded slightly smaller than finger discs (fig. 2). An elliptical inner metatarsal tubercle slightly larger and slightly less protuberant than round outer metatarsal tubercle. One to three rounded subarticular tubercles (one each on toes 1, 2, two each on 3 and 5, three on toe 4); the basal subarticular tubercles on toes 1–3 and 5 tend to be more prominent than all others. A weak tarsal keel extending from inner metatarsal tubercle for about one-third the length of tarsus, ending in a small round tarsal tubercle. Ventrolateral edges of digits keel-like, with keel from outer edge of toe 5 extending weakly onto foot toward outer metatarsal tubercle.

COLOR PATTERN: In life (fig. 1), dorsal surfaces of head and body black with variable spotted to lineate pattern (fig. 3) of vivid white markings. Limbs black with a less variable pattern of conspicuous markings of brilliant golden orange, as follows: A bandlike orange spot on dorsal and posterior sides of base of upper arm; a large orange spot extending dorsally across base of thigh from its anterior face; a large orange marking (calf spot) on proximoventral and anterodorsal part of

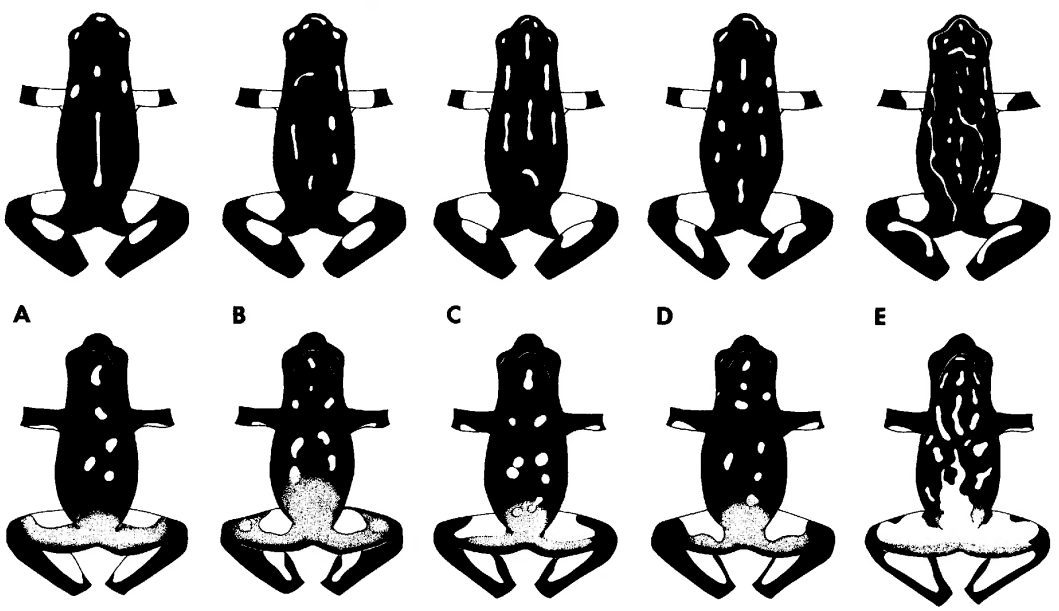

Fig. 3. Dorsal and ventral color-pattern variation in *Dendrobates castaneoticus*, new species. **A**, paratopotype (MZUSP 64766 ♂); **B**, holotype (MZUSP 64775 ♀); **C**, paratopotype (MZUSP 64769 ♀); **D**, paratopotype (AMNH 133453 ♂); **E**, paratype from Taperinha (MZUSP 30767 ♀).

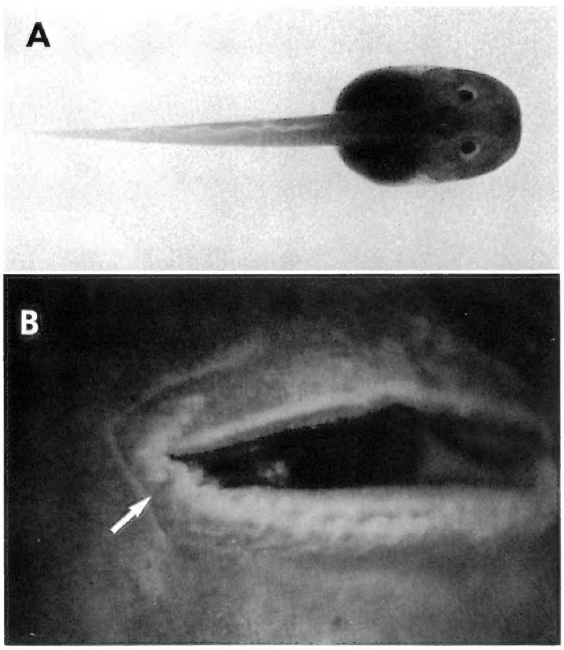

Fig. 4. **A**, Free-living tadpole of *Dendrobates castaneoticus*, new species, stage 27 (AMNH 133456); dorsal view ×3. **B**, Edge of oral disc of above tadpole, showing slight indentation (arrow) when mouth is nearly closed, ×30.

shank. Many specimens with a small whitish spot atop lower arm near hand; anterior surface of tarsus and top of foot with small areas of dull orange. Ventral ground color very dark gray to black, with pattern of white markings that are less vivid than on dorsum. Iris of eye appears black in daylight. In preservative, the orange coloring of the limbs fades and the frogs are black with white markings overall.

There seems to be ontogenetic change in the ventral color pattern: Two small juvenile paratopotypes 12.3–12.7 mm SVL (MZUSP 64771, 64777) have dorsal patterns like adults, but no pale belly markings. The throat and chest are dark gray, with a median white line running the full length of the throat. This pale gular stripe is better developed than the occasional median white marking of adults (being approached only in MZUSP 64764, which has a short gular line).

There also may be geographic variation in color pattern, since the two paratypes from Taperinha have more lineate dorsal patterns than those from the type locality. One of the Taperinha specimens (MZUSP 35681) has

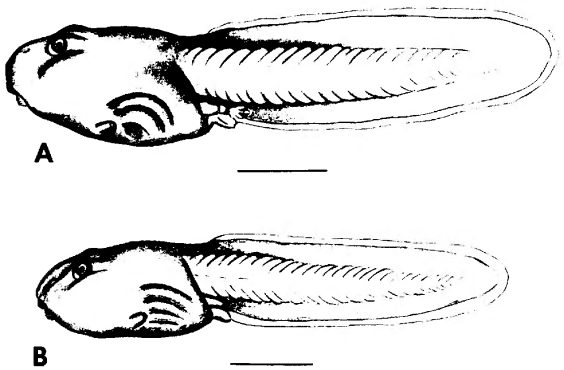

Fig. 5. Free-living tadpoles; scale lines = 5 mm. **A**, *Dendrobates castaneoticus*, new species, stage 35 (MZUSP 67201), from type locality. **B**, *Dendrobates quinquevittatus*, sensu stricto, stage 31 (AMNH 124072), from Alto Paraíso, Rondônia, Brazil.

rather straight lines and somewhat resembles the paratopotype in figure 3C, but the median and dorsolateral lines are appreciably longer than in the figured specimen. The other Taperinha paratype (MZUSP 30767) is shown in figure 3E; this relatively dense pattern of curving white lines is not approached by any other specimen in the type series.

Tadpoles

Tadpole carrying by nurse frogs was not observed, but free-living larvae (figs. 4, 5A) were collected in adventitious pools on the forest floor, especially in rain-filled fruit capsules from Brazil nut trees (see Distribution and Natural History below).

Habitus, Proportions, and Measurements: Head-body and total length measurements of 36 tadpoles in stages 24–45 are summarized in table 2. The following description is based mainly on the stage-35 tadpole (MZUSP 67201) shown in figures 5A and 6A. It is 30.9 mm in total length, 11.8 mm in body length. The body is depressed (body depth 74% of width), and from above is elliptical in shape, with a gently truncated snout (as in fig. 4); the snout is round in lateral view. The nostrils are situated dorsally, 1.9 mm from the midpoint of the snout, and directed anterolaterally; internarial distance is 1.8 mm, with each nostril situated on a line drawn from the outer edge of the eye to the midpoint of the snout. The eyes are dorsal, directed

TABLE 2
Measurements (in mm) of *Dendrobates castaneoticus* Larvae

Gosner stage	N	Body length mean ± 1 SD	Total length mean ± 1 SD
24	1	4.80	13.76
25	8	5.57 ± 0.53	14.94 ± 1.22
26	10	6.43 ± 0.61	16.79 ± 1.41
27	7	8.27 ± 0.86	21.52 ± 1.62
28	3	8.85 ± 0.96	23.59 ± 1.40
29	1	8.81	23.19
31	1	9.32	25.14
35	2	10.96 ± 1.22	28.33 ± 3.58
39	1	11.20	29.56
43	1	—	12.44 (SVL)
45	1	—	10.69 (SVL)

anterodorsally, and the interocular plane (line connecting anteriormost points of eyes) is 3.1 mm posterior to the snout; eyeball diameter is 1.5 mm and the minimum distance between eyes is 1.8 mm. The spiracle is sinistral and situated low on the body, 7.8 mm posterior to the snout; it is tube-shaped, but not free from the body. The anal tube is 1.5 mm long and dextral in orientation in this specimen. The anal tube usually is medial in *castaneoticus* larvae but may also be sinistral or dextral: In 28 larvae coded for this character, the anal tube is medial in 18 (64.3%), dextral in 6 (21.4%), and sinistral in 4 (14.3%).[6]

The tail is 19.1 mm in MZUSP 67201, comprising 61.8 percent of total length. The caudal musculature is 3.5 mm deep at the base of the tail and decreases only slightly until the posterior one-third of the tail, from which point the musculature gradually tapers to a rounded tip. Dorsal and ventral tail fins are low and nearly equal in height. At the midpoint of the tail, the dorsal fin is 1.8 mm high (58% of musculature height) and the ventral fin is 1.7 mm. The dorsal fin originates 1.2 mm behind the junction of body and tail. The tip of the tail is broadly rounded.

[6] A sinistral anal tube also has been noted in a stage-25 larva of the related *Dendrobates reticulatus* (AMNH 103706), along with essentially medial conditions in other stage-25 specimens (AMNH 103704, 103705). The tube is normally thought of as medial in *Dendrobates* and dextral in all other dendrobatids, with the rare sinistral condition being so far known only in the variation of the *Dendrobates quinquevittatus* complex. But to further complicate the value of this character, there are suggestions of ontogenetic change—from dextral to medial in *Epipedobates silverstonei* (Myers and Daly, 1979: 9), and from medial to dextral in *Phyllobates* spp. (Myers et al., 1978: 317; Donnelly et al., 1990)—but these trends need to be confirmed with larger samples.

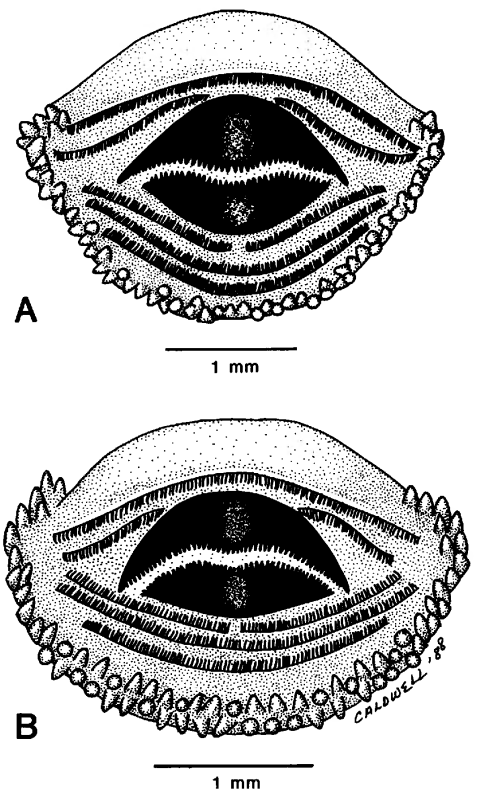

Fig. 6. Tadpole mouths. **A**, *Dendrobates castaneoticus*, new species, stage 35 (MZUSP 67201), from type locality. **B**, *Dendrobates quinquevittatus*, s.s., stage 31 (AMNH 124072), from Alto Paraíso, Rondônia, Brazil.

PIGMENTATION: In life, the tadpoles have dark gray bodies. The tail musculature and tail fins are lighter gray, with the tail fin being outlined by a narrow transparent border. In preservative, the body is dark gray dorsally, the chest is dark gray, and the remainder of the ventral surface of the body is transparent to opaque. The tail is brownish gray, with the musculature and upper fin being more heavily pigmented than the lower fin, which may have a lightly pigmented to clear area proximally. The transparent border of the tail fin remains distinct in preservative.

MOUTH PARTS: The anteroventrally situated oral disc of MZUSP 67201 (fig. 6A) has a maximum width of 3.3 mm. There are 2/3

tooth rows, with the second anterior (A-2) row conspicuously broken above the beak and the first posterior (P-1) row narrowly broken below the beak (fig. 6A). The very small P-1 gap was present in 27 (87.1%) of 31 larvae examined, but the broad A-2 gap was present in all. The three posterior tooth rows are slightly shorter than A-1. The anterior edge of the oral disc is nude, but its lateral and posterior edges bear one irregular row of papillae that becomes two rows in some places (fig. 6A). The beak is robust with serrated edges; both upper and lower jaws are heavily keratinized for nearly half their widths on the sagittal plane.

Figure 6A shows an oral disc that appears laterally unindented. However, *castaneoticus* larvae do have a weak infolding or indentation at the corner of the nearly closed mouth, as shown in figure 4B; this emargination may be weakly maintained or may completely disappear when the mouth is fully opened.[7]

Distribution and Natural History

Dendrobates castaneoticus occurs on the south side of the Amazon River in the state of Pará, northern Brazil. It is known only from the vicinity of the type locality and from Taperinha, nearly 300 km to the northwest of the type locality. Taperinha is only about 12 km from the Amazon River, east of the mouth of Rio Tapajós. The type locality is about 220 km south of the Amazon, in tropical lowland rain forest adjacent to the Rio Xingu. It is a closed-canopy forest of moderate height. Bromeliads and other epiphytes are relatively sparse. Spiny palms and stilt palms are conspicuous elements. Large and small individuals of the Brazil nut tree, *Bertholletia excelsa*, are widely spaced throughout the forest. This forest, especially during the wet season, is drained by numerous small streams, some fast flowing and others barely moving.

The species was uncommon at the type locality during the period of fieldwork, which coincided with the beginning of the rainy season in January and concluded in March. There were no observations of courtship, egg clutches, or transport of tadpoles, nor was the call of the species definitely identified. Four observers were in the forest nearly every day for two months, yet only 15 adults, 2 juveniles, and 36 tadpoles were collected.

Dendrobates castaneoticus is diurnal; all specimens were collected during the day and none was seen at night. A soft buzzing call possibly belonging to this species was heard deep beneath leaf litter during the day on several occasions, but the animal producing the call could not be located. Of the 17 specimens collected at the type locality, all but two were on the forest floor. One adult male not at ground level was foraging 1.5 m aboveground on hanging tree roots; a female was 0.5 mm up on a log approximately 30 cm in diameter. Another frog, not collected, was seen in a tangle of dead limbs approximately 1 m aboveground (L. J. Vitt, personal commun.). Although they obviously climb, hand size is relatively moderate and does not suggest any strong commitment to arboreal habits.

Six adult females, all with enlarged oviducts, had an average of 1.2 ± 1.2 (range, 0 to 3) greatly enlarged brown eggs in the right oviduct; thus, assuming eggs are contributed from both ovaries during oviposition, probable clutch size is 1–6, a figure consistent with other small species of *Dendrobates* and *Minyobates*. The six specimens had complements of 0–3 ($\bar{x} = 1.3 \pm 1.2$) smaller gray ovarian eggs, evidently representing development of the next clutch. Again, probable clutch size seems to be 1–6. All females also had many small white follicles in the ovaries. *Dendrobates castaneoticus* may be presumed to deposit multiple clutches at least during the rainy season.

Of 24 tadpoles found under natural conditions, 18 (75%) occurred individually in fallen fruit capsules of the Brazil nut tree, suggesting that nurse frogs carry only one tadpole at a time. The other six naturally occurring tadpoles were found in basins of water formed in the large petioles of fallen palm fronds. In the palm fronds, which held 4–5 times as much water as fruit capsules, up to three tadpoles were found in the same frond, along with numerous tadpoles of *Epipedo-*

[7] The primitive condition for dendrobatid larvae seems to be a lateral indentation that is conspicuously maintained even when the mouth is fully opened (e.g., see the drawings for eight species of *Phyllobates* and *Epipedobates* in Silverstone, 1976: 16).

bates femoralis and *Colostethus marchesianus*. The *D. castaneoticus* tadpoles invariably were of different sizes, again suggesting that they were transported at different times. Further evidence for transport of single tadpoles was provided by artificial containers placed in the forest. Eleven tadpoles were deposited by unseen nurse frogs in four plastic basins 30 cm in diameter, with a water depth averaging 10 cm. These basins were checked for new tadpoles every 48 hours. Although one basin ultimately had five larvae and three had two each, all these tadpoles appeared in the basins on different days.

The tadpole of *D. castaneoticus* has a robust beak and was observed to catch and consume mosquito larvae, an obvious and abundant food source in fallen water-filled fruit capsules of the Brazil nut tree. There was no evidence that females provided nutritive eggs to their tadpoles.

A possible instance of predation by a ctenid spider was noted. These ambush predators occasionally were seen lurking just inside the openings of Brazil nut fruit capsules on the forest floor. In February, while taking measurements on fruit capsules in a study plot, Caldwell and Vitt found a large spider and a dead male *Dendrobates castaneoticus* (MZUSP 64767) in the same fruit capsule. The frog had dorsal punctures but was otherwise unmarked; it was not ascertained whether the feeding sequence was interrupted by the observers or whether the frog had been killed earlier and rejected.

Caldwell (MS.) studied interactions with potential tadpole predators in Brazil nut fruit capsules. She found that *D. castaneoticus* larvae were seldom associated with aquatic predators (insect larvae) and were free of tail damage, raising the intriguing but unverified possibility that nurse frogs might somehow avoid placing tadpoles in predator-occupied fruit capsules.

Relationships

The closest known relative (sister species) of *Dendrobates castaneoticus* seems to be *D. quinquevittatus* sensu stricto. As redefined herein, *quinquevittatus* is a smaller Amazonian frog occurring in the upper Rio Madeira drainage well over 1000 km to the southwest of *castaneoticus*.

There is little indication of relationship in the very different color patterns of these two species, except that each has an iridescent orange or golden spot at the dorsal limb insertions (cf., figs. 1, 7). There is, however, one morphological resemblance that seems to be novel among dendrobatids: The inner metacarpal tubercle is, so far as we have noticed, a ubiquitous structure in the Dendrobatidae, except that it is absent *D. castaneoticus* and absent or vestigial in *D. quinquevittatus* s.s. The absence of this tubercle in the Dendrobatidae must therefore be judged as apomorphic loss, and its shared absence in two small Amazonian *Dendrobates* is a persuasive indication of relationship.

A few other resemblances between *D. castaneoticus* and *D. quinquevittatus* s.s. are worth noting: Their tadpoles seem virtually identical (figs. 5, 6), and both species often use fallen fruit capsules of the Brazil nut tree as tadpole deposition sites. These resemblances might seem at first sight to support our hypothesis of close (sister species) relationship between *castaneoticus* and *quinquevittatus*. But some degree of the larval resemblance will probably prove to be plesiomorphic, and other species of the *quinquevittatus* complex seem unlikely to ignore rain-filled fruit capsules as potentially good places to deposit tadpoles.

REVISIONARY NOTES ON THE *QUINQUEVITTATUS* GROUP

Silverstone (1975) recognized *Dendrobates quinquevittatus* as a highly variable species of small poison frog occurring throughout Amazonia. Myers (1982) partially revised the species, pointing out that museum specimens considered by Silverstone as *quinquevittatus* included a minimum of five species. Myers noted the availability of old names for two of these (*D. fantasticus*, *D. reticulatus*), described two others as new (*D. captivus*, *D. vanzolinii*), and implied (p. 14) the existence of another unnamed species "in the Huallaga and upper Marañón drainages of Andean Peru." Based on a synapomorphy of color pattern (distinctive limb reticulation), Myers erected a *quinquevittatus* species group for four species: *D. quinquevittatus* Steindachner, *D. fantasticus* Boulenger, *D. reticulatus*

Boulenger, and *D. vanzolinii* Myers. Left outside of this group was *Dendrobates captivus* Myers, which seemed possibly related to *D. mysteriosus* Myers (these two species may provisionally be referred to a *captivus* species group). Lötters (1988) wanted to redefine the residual *D. quinquevittatus* sensu Myers, but he perpetuated from Silverstone such worthless (i.e., composite) data as "14.5–21.5 mm" SVL, the lower end of this size range being based on *D. captivus* and with several other species contributing to the remainder (Myers, 1982: 14).

The changes made by Myers did not appreciably decrease the geographic range of *D. quinquevittatus*. But based on the original description and our 1985 fieldwork in Rondônia, we now realize that Myers (p. 1) erred in concluding that the restricted *quinquevittatus* remained "indeed a widespread and variable species." We correct that mistake by further restricting the name *Dendrobates quinquevittatus* Steindachner to a not particularly variable species confined to the southwestern section of Amazonia and by formally resurrecting the name *Dendrobates ventrimaculatus* Shreve for the residue of what recently has been called *quinquevittatus*. These changes were anticipated by Daly, Myers, and Whittaker (1987: 1025, 1085, 1087), who applied without comment the names *quinquevittatus* and *ventrimaculatus* as used herein.

We emphasize that *Dendrobates ventrimaculatus* sensu lato becomes the new composite species of this complex, but we urge caution in dealing with it systematically. We are aware that "*ventrimaculatus*" contains more than one species, some of which may be difficult to separate even when sympatric (G. Vigle and C. W. Myers, unpubl.). Attempts at taxonomic diagnosis based on literature and/or terrarium specimens of vague provenance seem likely to be fruitless at best (e.g., Lötters, 1988), or, more seriously, to create needless confusion arising from nomenclatural irresponsibility.

Dendrobates quinquevittatus Steindachner
Figures 5B, 6B, 7, 8B, 9

Dendrobates quinquevittatus Steindachner, 1864: 260–262, pl. 15, fig. 2 (holotype in dorsal view). Holotype: NMW 16517 [fide Silverstone, 1975; Häupl and Tiedemann, 1978] from Salto do Girao [= Salto do Jirau, Rondônia], Brazil, collected by Johann Natterer, October 11, 1829.

Dendrobates tinctorius var. *quinquevittata* Steindachner, op. cit.: 288 (in caption to pl. 15, fig. 2, vide supra).

Fig. 7. *Dendrobates quinquevittatus* Steindachner (sensu stricto). A specimen (AMNH 124068 ♀) from Alto Paraíso, Rondônia, Brazil, approximately ×3; from a color transparency by C. W. Myers.

NEW DIAGNOSIS: A small toothless dendrobatid attaining a maximum length of about 20 mm SVL, with appressed first finger shorter than second and with the inner metacarpal tubercle absent (fig. 8B) or vestigial. Head and body black with five conspicuous light blue (or pale greenish or yellowish) lines, throat and venter pale bluish (or greenish) white with irregular black spots; arms and legs dull orange dorsally and ventrally, with a small gold or metallic orange spot dorsally at limb insertions and with well-separated small black spots (fig. 7). This combination of characters separates *D. quinquevittatus* from all other dendrobatids.

Dendrobates quinquevittatus shares with *D. castaneoticus* the presence of an iridescent orange or golden spot at the dorsal limb insertions (cf., figs. 1, 7), absence of a bright chin spot, and absence of the inner metacarpal tubercle, but the lineate dorsal pattern and dull orange limbs of *quinquevittatus* immediately distinguish it from the larger *castaneoticus*.

Dendrobates quinquevittatus is readily dis-

TABLE 3
Size and Proportions of *Dendrobates quinquevittatus* Steindachner from Upper Rio Madeira drainage, Brazil[a]

Character[b]	N	Mean	Range
Snout–vent length in mm	5 ♂	16.88	16.0–17.5
	6 ♀	18.98	18.3–20.2
Tibia length/SVL	4 ♂	0.450	0.43–0.46
	6 ♀	0.448	0.43–0.47
Head width/SVL	4 ♂	0.329	0.31–0.34
	6 ♀	0.321	0.31–0.33
Naris-edge eye/eye	4 ♂	0.786	0.76–0.81
	6 ♀	0.784	0.72–0.86
Hand length/SVL	4 ♂	0.253	0.23–0.28
	6 ♀	0.253	0.24–0.27
Hand length/head width	4 ♂	0.768	0.74–0.80
	6 ♀	0.788	0.73–0.84
3rd-finger disc/finger	4 ♂	1.925	1.75–2.20
	6 ♀	1.806	1.60–2.00

[a] A nonhomogeneous sample from four widely separated localities in Rondônia (fig. 10) and one in Amazonas, as follows: Alto Paraíso (N = 3), Nova Brasília (1), Sta. Bárbara (5), Sta. Cruz da Serra (1), Igarapé Puruzinho, Amazonas (1). The 10 specimens from Rondônia may include subadults of both sexes as well as adults (see text); one of the males is a skinned carcass measured only for SVL.

[b] See notes to table 1 for methods of measuring certain characters.

tinguished from most of its other close relatives (including populations previously assigned to *quinquevittatus*) by absence of a pale reticulum (or close-set spots) on dorsal and ventral limb surfaces, by absence of a bright chin spot (i.e., underside of head same color as belly), and by absence of the inner metacarpal tubercle (sometimes vestigial, see Discussion). The distinctive limb color pattern of *D. quinquevittatus* s.s. is approached, however, in certain dendrobatid populations in Huánuco, Peru (see Discussion under *D. ventrimaculatus*).

NOMENCLATURAL HISTORY AND TYPE LOCALITY: "*Dendrobates quinquevittatus* Fitz. Tschudi, Mus. Vind." was a Fitzinger and/or Tschudi manuscript name that was first published in the synonymy of *Dendrobates tinctorius* by Steindachner (1864), who is the sole author for nomenclatural purposes since he alone was responsible for publishing the name and a validating illustration (see also art. 50g, 1985 *Internatl. Code Zool. Nomencl.*). The name was not published as a "true" synonym in the modern sense because Steindachner treated it as one of the "Varietäten" of *tinctorius* and the name therefore has always been legally available (Myers, 1982: 3).

The single specimen (holotype) available to Steindachner was said to have been found by "Joh. Natterer bei Salto do Girao am 11 October 1829." This locality (including the variant spellings *Salto de Girão* and *Salto do Girâo*) is now known as Salto do Jirau; it is situated on the Rio Madeira, at 9°20'S, 64°43'W, in the modern State of Rondônia. Corroboration of this locality and date can be found in Natterer's itinerary published by Pelzeln ("1871" [1868–1870]: xii). We have not examined the holotype of *Dendrobates quinquevittatus*, but Steindachner's illustration and the accompanying color notes from life (see below) leave no doubt that it is the same species being redescribed here and there is reasonable proximity between the type locality and the new records of *D. quinquevittatus* (fig. 10). Furthermore, Martin Henzl (in litt.) has kindly examined the holotype and found "absolutely no trace of an inner metacarpal tubercle."

NEW DESCRIPTION

SIZE AND MORPHOLOGY: Two adult males with paired vocal slits are 17.0 mm and 17.5 mm SVL; three subadult or possibly adult males with vocal slits not developed are 16.0, 16.4, and 17.5 mm SVL. Three adult females with enlarged oviducts and ova are 18.6 mm, 20.0 mm, and 20.2 mm SVL; three subadult or sexually inactive adult females are 18.3, 18.3, and 18.5 mm SVL. Measurements and standard proportions are summarized in table 3.

Dorsal skin finely granular or smooth in preservative, ventral skin smooth or moderately granular on belly. Width between outer edges of upper eyelids only slightly smaller than (< 0.6 mm) head width between jaw articulations. Snout sloping, rounded in profile, rounded to nearly truncate in dorsal or ventral view. Nares situated near tip of snout and directed posterolaterally; both nares visible from front and from below, not visible from above. Canthus rostralis rounded; lo-

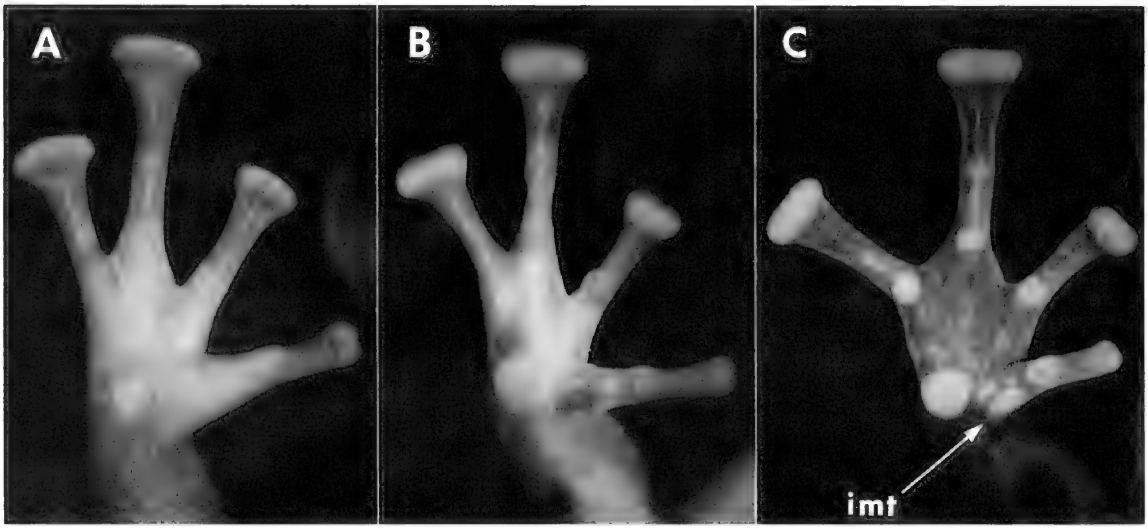

Fig. 8. Left hands, showing presence of the inner metacarpal tubercle (imt) in C and its derived absence in A and B. **A**, *Dendrobates castaneoticus*, new species (MZUSP 64776, ad. ♂ paratype). **B**, *D. quinquevittatus*, sensu stricto (AMNH 124069, ad. ♂), Alto Paraíso, Rondônia, Brazil. **C**, *D. ventrimaculatus* (USNM 266119, ad. ♂), Cachoeira Nazaré, west bank Rio Jiparaná, Rondônia, Brazil.

real region vertical and flat. Interorbital area wider than upper eyelid. Eye shorter than snout length in lateral view; distance from naris to eye 72–83 percent of eye length (table 3). Tympanum concealed dorsally and posterodorsally, much smaller than eye.

Hand (fig. 8B) of moderate size, 23–28 percent of SVL, 73–84 percent of greatest head width (table 3). Relative length of *appressed* fingers 3 > 4 > 2 > 1; appressed first finger moderately long, its tip approaching or reaching disc of second finger. Discs markedly expanded on all except first finger. Third finger disc 1.6–2.2 times wider than distal end of adjacent phalanx, averaging wider in males than in females (table 3). All specimens with a single metacarpal tubercle—i.e., a circular outer metacarpal tubercle present on base of palm, but inner metacarpal tubercle absent (fig. 8B) or vestigial (see following Discussion for description of variation). One or two rounded, prominently raised subarticular tubercles (two on finger 3, with distal one less prominent, one each on fingers 1, 2, and 4, sometimes with weak indication of a distal second tubercle on finger 4). Ventrolateral edges of digits slightly keeled, with keel from outer edge of finger 4 extending weakly onto hand to metacarpal tubercle.

Hind limbs relatively short, with heel of appressed limb usually reaching or almost reaching tympanum. Tibia length 43–47 percent of SVL in adults (table 3). Toes not webbed. Relative lengths of appressed digits 4 > 3 > 5 > 2 > 1; first toe not particularly short although only reaching proximal edge of subarticular tubercle of second toe. First toe with nonexpanded disc, other toes with moderately expanded discs. Inner and outer metatarsal tubercles usually subequal, small, and relatively prominent. One to three rounded subarticular tubercles (one each on toes 1, 2, two each on 3 and 5, three on toe 4); the basal subarticular tubercles on toes 1–3 and 5 tending to be more prominent than all others. Tarsal tubercle present, sometimes faint; tarsal keel absent (one specimen with a faint indication adjacent to tarsal tubercle). Ventrolateral edges of digits keel-like, with keel from outer edge of toe 5 extending onto foot towards outer metatarsal tubercle.

Color in Life and Pattern Variation: Steindachner's dorsal-view illustration of the 160-year-old holotype agrees well with the specimens that we collected in Rondônia, except that the type seems to have somewhat wider dorsal and dorsolateral lines. The pattern of the limbs (pale with well-separated spots) seems diagnostic and is well shown in the illustration of the holotype. Color notes

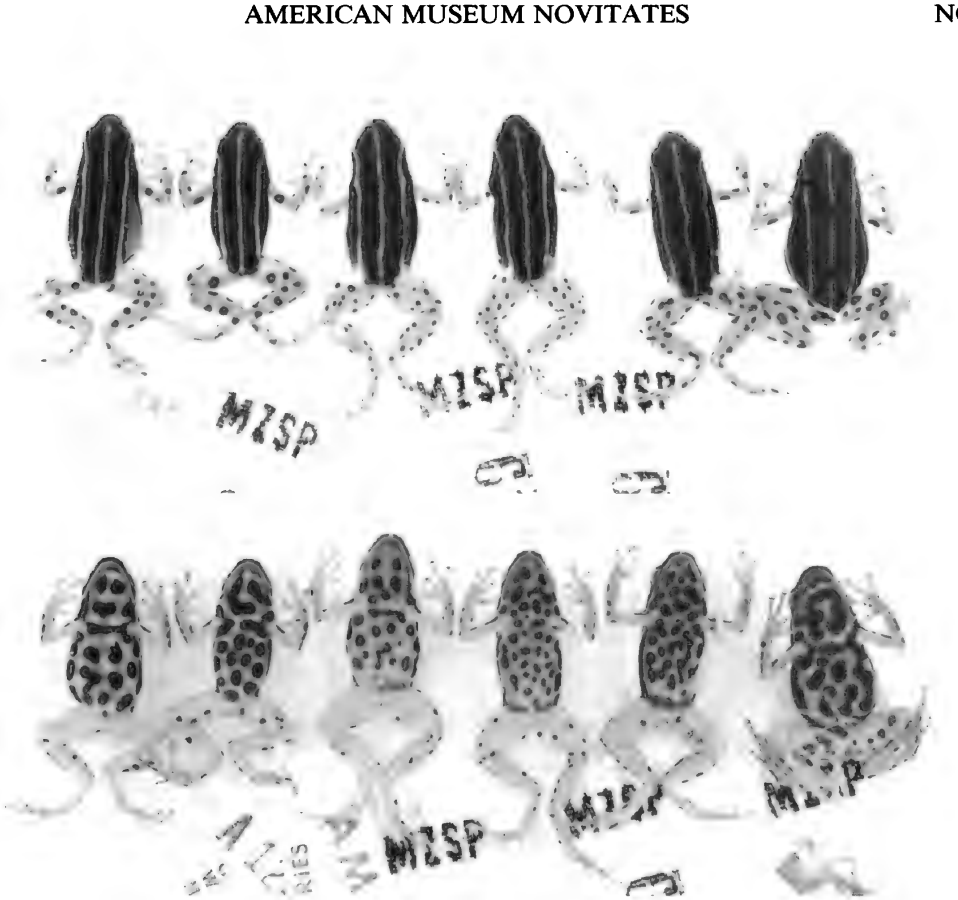

Fig. 9. Dorsal and ventral color-pattern variation in *Dendrobates quinquevittatus* s.s., from upper Rio Madeira drainage, Brazil, ×1.2. From left to right: AMNH 124068 ad. ♀, 124069 ad. ♂, MZUSP 61795 ♀, 61797 ♀, 61798 ♀, USNM 201860 ad. ♀. First two specimens from Alto Paraíso, Rondônia, next three from Santa Bárbara, Rondônia, last specimen from Igarapé Puruzinho, Amazonas.

on living adult and subadult specimens from Rondônia were made by Natterer at Salto do Jirau in 1829 (see Steindachner, 1864: 261), by Caldwell at Santa Bárbara (May 1985), by R. I. Crombie at Nova Brasília (Nov. 1984), and by Myers at Alto Paraíso (October 1985). These independent accounts are remarkably similar, with the few differences being indicated in the following composite description:

In life (fig. 7), head and body black with five pale stripes (light blue according to our notes, faintly greenish fide Crombie, yellowish white fide Natterer); throat and venter pale blue (faintly greenish fide Crombie, yellowish white fide Natterer) with irregular black markings. Arms and legs orange (Caldwell), dull orange (Crombie and Myers), or dirty orange (Natterer) above and below, with well-separated small black spots at least on the dorsal limb surfaces; an ill-defined albeit conspicuous small spot of bright gold (Myers), iridescent or bright orange (Caldwell and Crombie), or orange-red (Natterer) at dorsal insertions of arms and legs. Iris black (Caldwell and Myers). Crombie's notes on a recently metamorphosed froglet (Cerejeiras, Nov. 1985) indicated dorsum black with yellow lines, ventral pale areas bluish, limbs bright orange above and below with black flecks.

Pattern variation is relatively slight in preserved specimens (fig. 9): The pale lines may be straight or slightly wavy. The median line usually originates on the head just in front of the eyes, but in two specimens there is an anterolateral extension (to the left on one, to the right on the other) connecting the median and dorsolateral lines; another specimen has two distinct breaks (1–1.5 mm long) in the median line. The dorsolateral lines are confluent on the tip of the snout, where one individual has a pale vertical line connecting

the dorsolateral and labial markings. The pale labial line extends posteriad usually over the arm insertion to connect with the lateral line, which may be discrete or which may have one to several connections with the pale belly color. The throat and venter are heavily patterned with irregularly shaped black markings on a white ground; several specimens have a narrow dark band across the ventral part of the waist (fig. 9); there is no pale chin spot of a color different from the ventral ground, and the dark gular markings frequently extend forward to the chin. The light-colored limbs are conspicuously marked with small round black spots that are mostly well separated; the spots are usually (in 8 of 9 specimens) greatly reduced or absent on the ventral surfaces of the limbs; hands and feet are colored like the limbs but tend to be only weakly dotted with black. The originally gold or iridescent orange spots on the dorsal insertions of the limbs are retained as small, very pale areas, which usually are free of black spotting.

TADPOLES: The tadpole is similar to that of *Dendrobates castaneoticus*, as can be seen by comparing illustrations showing shape and color pattern (fig. 5) and mouth parts (fig. 6).

DISTRIBUTION AND NATURAL HISTORY

Dendrobates quinquevittatus s.s. occurs in southern Amazonia, in the Rio Madeira drainage of western Brazil. At present, we know it definitely from localities in Rondônia (fig. 10) and from one site in adjacent Amazonas. The last locality is 130 km almost due north of the northernmost locality (Santa Bárbara) shown in figure 10. The distribution as now known falls between parallels 7 and 14° South, and meridians 60 and 65° West.

The habitat is lowland rain forest. The frogs were seen by day mostly on fallen logs and nearby leaf litter, also on tree buttresses and stumps to at least 1 m aboveground. It is a shy and hard-to-catch frog, leaping off logs or tree buttresses and disappearing quickly into the leaf litter. In nine days of forest collecting at Alto Paraíso, Myers and R. I. Crombie saw only six frogs, three of which managed to outwit the supposedly experienced collectors. L. J. Vitt (personal commun.) noted that, at Santa Cruz da Serra, it took him a half-hour to catch a single frog after dislodging it from under a rock by day. Apparent uncommonness at Alto Paraíso and at Santa Cruz da Serra may have been partly due to exceptionally dry weather during the periods of collecting. At Santa Bárbara, Caldwell and Vitt obtained six specimens at night by moving palm litter on the floor of shallow rock caves.

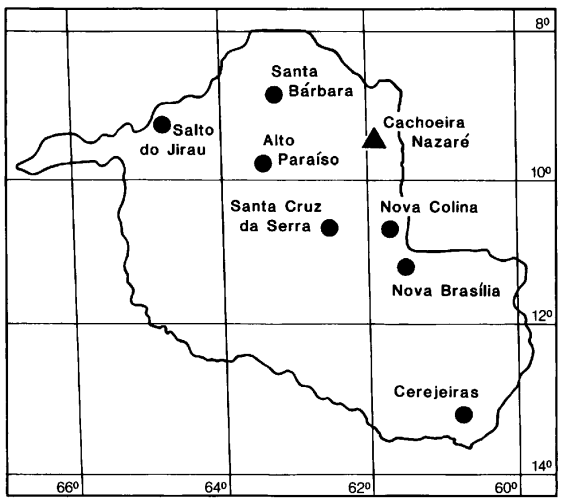

Fig. 10. Rondônia, Brazil, showing localities for *Dendrobates quinquevittatus* s.s. (circles) and *Dendrobates ventrimaculatus* s.l. (triangle). Map adapted from Vanzolini (1986: 9). One additional locality known for *D. quinquevittatus* s.s. is Igarapé Puruzinho (Amazonas) on the Rio Madeira—130 km north of Santa Bárbara.

We did not hear the call of *D. quinquevittatus*. Crombie and Myers found free-living tadpoles in several kinds of phytotelmata in October and November (the only season of fieldwork, in 1984 and 1985): At Alto Paraíso, a total of seven larvae were taken from two water-filled holes atop a palm stump and a tree-stump (≃ 1 m high); an adult frog was seen in one of these holes. At Cerejeiras, three larvae and a juvenile were in a dead stump cavity and two other larvae were in a rolled palm frond on the ground. At Nova Colina, a dozen tadpoles were found in fallen Brazil nut fruit capsules—one capsule with three larvae and nine capsules with one larva each. At Santa Cruz da Serra, larvae were found in the water-filled crevice of a log, and two other larvae were together in a single Brazil nut fruit capsule on the forest floor.

All the preceding samples of larvae are cat-

aloged in the AMNH and USNM collections (although not all the latter are cited under Specimens Examined); identity of several samples was confirmed by froglets raised to metamorphosis by R. I. Crombie (personal commun.). Although Brazil nut fruit capsules are commonly used, *Dendrobates quinquevittatus* seems to deposit tadpoles in virtually any available phytotelmata on or near the forest floor.

Discussion

Dendrobates quinquevittatus s.s. and *D. ventrimaculatus* s.l. both occur in Rondônia (fig. 10). The specimens (MZUSP 63792, USNM 266119) of "*ventrimaculatus*" from Rondônia have two unpigmented metacarpal tubercles on darkly pigmented palms, which makes the smaller inner tubercle easy to distinguish (fig. 8C). However, the base of the thumb may be pure white in "*ventrimaculatus*" from some other populations (see fig. 12), and it would be easy to overlook the small inner tubercle if the hand is not carefully examined under good light and high magnification.

Although the inner metacarpal tubercle seems completely absent in the new *D. castaneoticus* and in most *D. quinquevittatus* (fig. 8A, B), possible vestiges of it were detectable in a few *quinquevittatus*: Under a magnification of ×50, this tubercle was coded as either absent or possibly represented by slight epidermal thickening on 17 of 20 hands (10 frogs), with possible vestiges on three other hands. Without reverting to histological examination, the best argument for presence of a vestigial tubercle is provided by AMNH 124068; the left hand shows a definite, albeit not well-defined, fleshy swelling at the base of the thumb, and the right hand in this location bears a better defined but much smaller pustulelike swelling about 0.1 mm in diameter. Even in these cases, however, the pigment cells on the base of the thumb appear quite superficial and are not overlain by a translucent calluslike patch of stratum corneum like the one covering the outer metacarpal tubercle.

Based on one skin from Alto Paraíso, *Dendrobates quinquevittatus* s.s. produces toxic alkaloids mainly of the histrionicotoxin and pumiliotoxin-A classes, with minor representation by decahydroquinoline and unclassified alkaloids. The single skin contained 17 different alkaloids (Daly et al., 1987: 1025, 1085).

Specimens Examined: **Amazonas:** Igarapé Puruzinho, Rio Madeira, 7°24'S, 63°00'W (USNM 201860). **Rondônia:** Alto Paraíso (AMNH 124068–124070, 124072 [tadpoles]); Cerejeiras (USNM 297742); Nova Brasília (USNM 297741); Nova Colina (USNM 297744, 297745–297753 [only tadpoles from this locality]); Santa Bárbara (AMNH 124071, MZUSP 61795–61799); Santa Cruz da Serra (AMNH 124073 [tadpoles], MZUSP 61309).

Dendrobates ventrimaculatus Shreve

Figures 8C, 11–12

Dendrobates minutus ventrimaculatus Shreve, 1935: 213–214. Holotype: MCZ 19734, from Sarayacu, Ecuador, collected by O. C. Felton in 1933.

Dendrobates ventrimaculatus Shreve. Daly et al., 1987: 1025, 1087.

Dendrobates variabilis Zimmermann and Zimmermann, 1988: 132–134. Holotype: SMNS 7054, from Departamento San Martín [no explicit locality given], Peru, collected by R. Schulte in 1983. NEW SYNONYMY.

Diagnosis: Shreve's name *Dendrobates ventrimaculatus* sensu stricto is formally revived from the synonymy of *D. quinquevittatus* for a species that has a pale reticulum on dark limbs, a bright chin spot (or entire throat) differing from the pale belly color (but same hue as the pale dorsal markings), inner metacarpal tubercle present, and smaller size.

Unfortunately, however, an unknown number of undiagnosed species share the aforesaid characters and so the name *ventrimaculatus* cannot be used in the strict sense with any confidence. But pending further study, *D. ventrimaculatus* sensu lato conveniently serves to accommodate various populations heretofore assigned to *quinquevittatus*.

For a variety of color patterns now subsumed within *D. ventrimaculatus* s.l. throughout its range—from Ecuador and Peru to the Guianas—see Duellman (1978: pl. 1), Meede, 1980 (figs. 2–4, 9), Myers (1982, figs. 1A, 7B), Lescure and Bechter, 1982 (all figs.

except fig. 22 [= *D. reticulatus*]), and this paper (figs. 11–12).

Discussion

G. Vigle and C. W. Myers (unpubl.) have reason to suspect the existence of a pair of sympatric sibling species in eastern Ecuador, one of which is thought to equal *ventrimaculatus* in the strict sense. Preliminary data on skin toxins have been obtained (additional to Peruvian samples already reported by Daly et al., 1987), but the calls and tadpoles of the Ecuadorian frogs are unknown. These kinds of data, however, can do no more than prove the existence of separate species—allocation of names is a separate problem currently under study and not yet resolved.

Certain central Peruvian specimens of *D. ventrimaculatus* s.l. approach the distinctive limb color pattern of *D. quinquevittatus* s.s.; these specimens (AMNH 43017, 43033; also Meede, 1980, figs. 3–4) are from the Río Pachitea drainage (Departo. Huánuco) and have rather widely spaced dark markings on pale limbs and a dorsal striped pattern. Most other Peruvian populations are characterized by a pale reticulum (fig. 11) or close-set dark spots (fig. 12) on the limbs, but dorsal patterns vary: For example, a dorsal reticulate pattern occurs at geographically distant sites, as shown in photographs published in Myers (1982, fig. 7B), in Schulte (1986), Zimmermann and Zimmermann (1988, fig. 3), and in this paper (fig. 11D).

Zimmermann and Zimmermann (1988) coined "*Dendrobates variabilis*" for one of the Peruvian populations without providing any type locality other than the distressingly vague "Departamento San Martin, Peru"—a topographically diverse area comprising over 45,000 km^2. The *nomenclatural* concepts of type locality and name assignment are especially important to the *biological* problems of analyzing complex variational and distributional patterns among species. Without a proper type locality it is difficult to start answering questions such as: Is the San Martín frog shown in our figure 11C likely to come from the same regional population as the holotype of *variabilis*? If not, what is the geographical proximity of the populations? Does gene flow seem likely or is there a formidable ecogeographic barrier? To what species would the name *variabilis* apply if two or more species with overlapping variation were detected? Vague or incorrect type localities accompanying names published over a century ago have caused enough such problems (e.g., *D. histrionicus*, *D. maculatus*, and *Phyllobates bicolor* as dendrobatid examples); geographic imprecision cannot be condoned in modern systematics.

The name *Dendrobates variabilis* is legally available, but the description has little to recommend it except a photograph (of a nonpreserved paratype) and a sound spectrogram. *Dendrobates variabilis* is based on the holotype (collected by R. Schulte in 1983) and an unspecified number of living paratypes, which also lack explicit locality data. There is virtually no description other than that of color pattern. There is a comparative sound spectrogram from *D. quinquevittatus*, which presumably = *D. ventrimaculatus* in the loose sense, but the geographic origin of the frog that made the call is not given and the usefulness of the spectrogram is therefore limited. Zimmermann and Zimmermann briefly but adequately differentiated *D. variabilis* from *D. imitator*, but Schulte (1986) had already done this rather thoroughly when he differentiated his new *imitator* from sympatric "*quinquevittatus*."

Dendrobates variabilis may prove to represent a species distinct from *D. ventrimaculatus* s.s., but at present it is not diagnosable from all other populations of *D. ventrimaculatus* s.l. Since the *variabilis* holotype was collected by Rainer Schulte, Zimmermann and Zimmermann's *variabilis* conceivably comes from a population sympatric with Schulte's *D. imitator*; Zimmermann and Zimmermann imply such sympatry but it must be confirmed with precise data. Schulte has been continuing his study of these frogs and may be able to clarify the matter. Meanwhile we relegate the name *variabilis* to what may be temporary synonymy, until such time that it can be diagnosed properly and distinguished from other reticulate *ventrimaculatus*.

Features of color pattern are nearly always useful in distinguishing species of dendrobatids, but determining species status even of populations with novel color patterns can

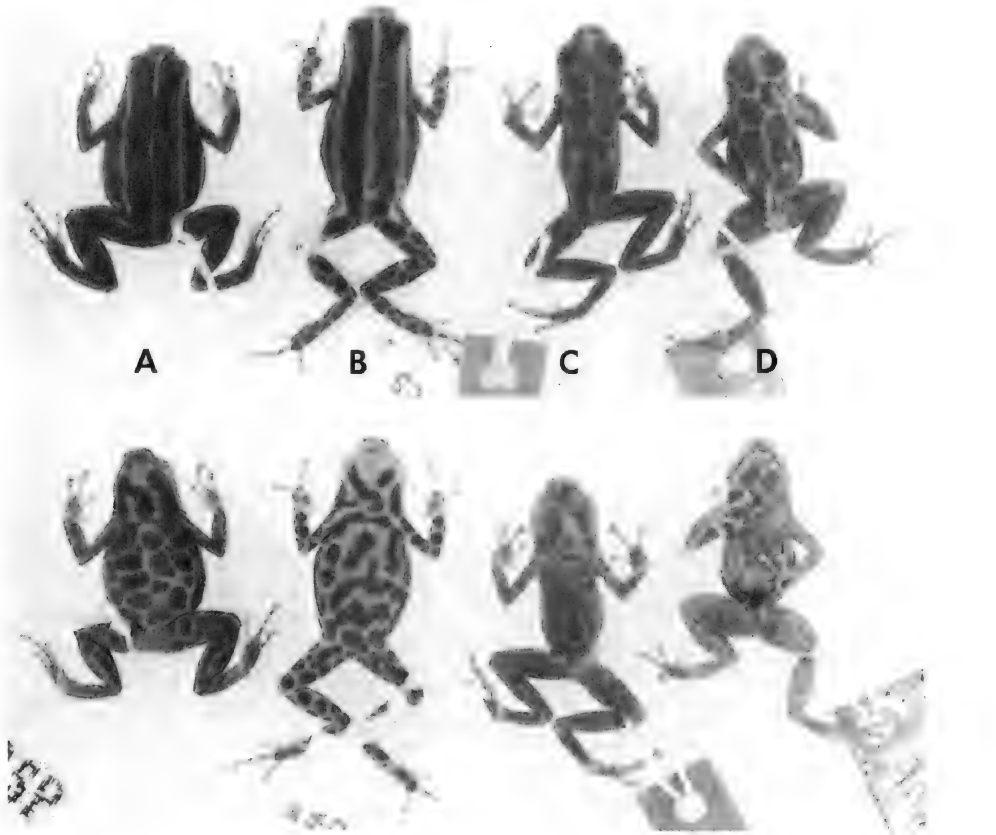

Fig. 11. *Dendrobates ventrimaculatus* s.l. A Brazilian specimen (A) from near southern limit of range, and three specimens (B–D) with diverse patterns from east-central Peru; dorsal and ventral views, ×1.5. **A**, Southern specimen (MZUSP 63792 ad. ♀) from Cachoeira Nazaré, west bank Rio Jiparaná, Rondônia (fig. 10). **B**, Boldly striped specimen (AMNH 91839 ad. ♀) from Tingo María, 670–770 m, Río Huallaga drainage, Huánuco. **C**, Partially reticulated specimen (AMNH 51315 ad. ♀) from Río Cainarche, about 200–450 m, Río Huallaga drainage, San Martín. **D**, Fully reticulated specimen (AMNH 60670 ad. or subad. ♂) from lower Río Pisqui, Ucayali drainage, Loreto.

be difficult in certain groups of *Dendrobates* (e.g., Myers and Daly, 1976: 222–225). And "*Dendrobates ventrimaculatus*" is such a group. Partially or completely reticulate dorsal patterns occur as variants in many parts of the range of "*ventrimaculatus*" (e.g., see Lescure and Bechter, 1982, fig. 21), but a completely reticulate pattern may be fixed in certain eastern Peruvian populations, particularly the one that is sympatric with *D. imitator* (see group photograph in Schulte, 1986: 14). We have seen only single specimens from some populations containing this type of pattern (e.g., Myers, 1982, fig. 7A; this paper, fig. 11D) and the problem of intra- and interpopulational variation needs resolving before drawing taxonomic conclusions from color pattern. Evidence of geographic continuity between such populations would of course provide a compelling argument for conspecificity, particularly if accompanied by a comprehensive survey of variation among other *ventrimaculatus*-like populations in eastern Peru.

A few examples of variation in *D. ventrimaculatus* s.l. from the southern half of eastern Peru are shown in figures 11B–D and figure 12. This region may lack at least one pattern variant that is common in northeastern Peru and other parts of the range (e.g., see Myers, 1982, fig. 1A, or Lescure and Bechter, 1982: 107).

Dendrobates ventrimaculatus s.l. has a broad distribution that remains essentially as

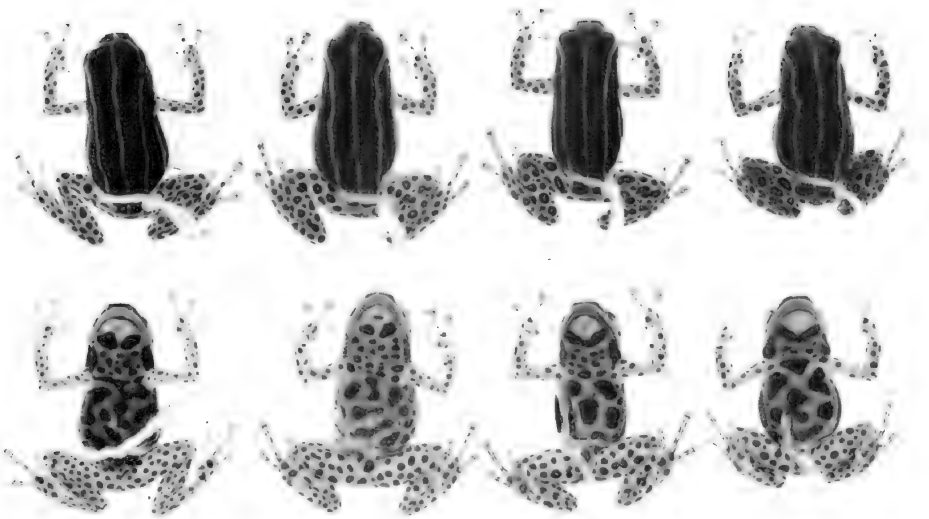

Fig. 12. Population sample of *Dendrobates ventrimaculatus* s.l. from near southern limit of range in Peru. Dorsal and ventral views, ×1.5; from left to right: USNM 268841 ad. ♂, 268842 ad. ♀, 268843 ad. ♂, 268844 ad. ♂. All from Tampopata, 280 m, 30 km airline SSW Puerto Maldonado, Madre de Dios, Peru.

large as mapped by Silverstone (1975, fig. 8, as *quinquevittatus*). Although we remove his single locality (for holotype of *quinquevittatus*) on the Rio Madeira, the range of *D. ventrimaculatus* nonetheless does extend south to the upper Madeira drainage. Two specimens (MZUSP 63792, USNM 266119) were taken by A. L. Gardner at Cachoeira Nazaré, 9°43'S, 61°55'W, on the Rio Jiparaná (= Rio Machado), some 100 km from our nearest *quinquevittatus* locality (fig. 10).

Lynch (1979) predicted that there probably "exist very few 'widely distributed' species of forest amphibians" and his short list (op. cit., table 8:1) of those occurring in more than one major forest region becomes still shorter (fide Zweifel and Myers, 1989: 14). The only dendrobatid in Lynch's list, *Phyllobates pictus* sensu Silverstone (1976), also is a composite of more than one species.[8] Other very broadly distributed South American dendrobatids are confined to Lynch's "central cis-Andean forests" (i.e., the Amazonian + Guayanan rain forests), and there is no particular reason to suspect that they are not what they seem. However, *Dendrobates ventrimaculatus* s.l. invites attention because of the variability within and among assigned populations. Although it is a composite species as treated herein, we cannot predict whether an ultimately restricted *D. ventrimaculatus* will have an appreciably smaller range or continue as a widespread Amazonian species. In either case, *ventrimaculatus*-like frogs are not ubiquitous elements of the Amazonian forest; they seem to be absent in large parts of central Amazonia, being not found, for example, at the type locality of *D. castaneoticus*.

SYSTEMATIC CONCLUSIONS

Dendrobates castaneoticus, new species, and the severely restricted *Dendrobates quinquevittatus* Steindachner seem to be sister species based on the shared loss of the inner metacarpal tubercle and on the shared pres-

[8] The recognition of *Epipedobates flavopictus* (Lutz) was only part of the solution (Myers, 1987: 303), and the current name *Epipedobates pictus* is still being applied to two or more distinct species.

ence of an iridescent orange or golden spot at the dorsal limb insertions. Myers (1982) had defined a *quinquevittatus* species group based on the synapomorphy of the pale limb reticulum, but *quinquevittatus* s.s. is now seen to lack that defining character, which also is somewhat variable among populations currently assigned to *D. ventrimaculatus*. A *quinquevittatus* species group may still be monophyletic in a broader sense—with *castaneoticus* + *quinquevittatus* s.s. standing as the plesiomorphic sister group to those species characterized by a pale limb reticulum or close-set spots (for content, see Myers, 1982 [the *captivus* group is not to be included, see p. 11 herein], and Schulte, 1986). We suggest as a working hypothesis that this larger assemblage is monophyletic, but emphasize that the *quinquevittatus* species group is now defined only by taxonomic content. Within that group we recognize *Dendrobates ventrimaculatus* s.l. as a composite species, the successful taxonomy of which will depend in large part on thorough studies of intrapopulational and geographic variation.

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Note added in proof

Dr. Nelson Jorge da Silva (personal commun.) informed us that *Dendrobates quinquevittatus* was recently found to be abundant during the flooding of a dam site in Rondônia. A specimen from the hydroelectric region of Samuel (8°45'S, 63°26'W) on the Rio Jamari—some 50 km E Porto Velho—is shown in color in the following article: Marcio Martins and Ivan Sazima, 1989, "Dendrobatídeos cores e venenos," Ciência Hoje, 9(53): 34–38. Their photograph agrees well with fig. 7 herein except that the frog's limbs are a lighter orange and the body stripes are whitish (vs. pale blue as in fig. 7), thus confirming the range of color variation suggested by available descriptions (see pp. 13–14). We wish to acknowledge that, based on a sample of frogs from this new locality, Marcio Martins and Celio F. B. Haddad (unpubl. MS.) have independently concluded that the name *D. quinquevittatus* Steindachner has been widely misapplied.

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